

Larval Foodplant and other Effects on Troidine Guild Composition (Papilionidae) in Southeastern Brazil

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Abstract. In two neighboring forest sites (Amarais and Monjolinho) in Campinas, São Paulo, Brazil, with different *Aristolochia* host plants, two guilds of the same six troidine swallowtail butterflies showed major differences in their relative species proportions. *Parides agavus* represented over half the adults marked in Monjolinho but only 3% of those in Amarais; *P. proneus* included over half the adults in Amarais, versus 3% in Monjolinho. These contrasting proportions remained essentially unaltered during a major macroclimatic anomaly (El Niño-Southern Oscillation) in 1982-1983, which however significantly altered the proportions of three other species, and permitted the occasional *P. neophilus* to become established and common in both sites. Troidine juveniles (a total of 1802) were located and followed during two years in Monjolinho. Introduction of *Aristolochia melastoma*, abundant in Amarais, into Monjolinho caused larvae and adults of the *melastoma*-specialist *P. proneus* to become more common there. No hostplant effects could be clearly identified, however, to account for the contrasting abundances of *P. agavus* in the two sites, which seem better correlated with dense vegetation structure and reduced understory illumination, affecting the microclimate in Monjolinho.

Introduction

Most species of the cosmopolitan butterfly family Papilionidae (swallowtails) occur in the tropics (Slansky, 1972; Collins & Morris, 1985). Larvae of some *Papilio* species are pests of *Citrus* (Rutaceae), and other swallowtails attack cultivated Lauraceae, Magnoliaceae, Annonaceae and Umbelliferae (Feeny et al., 1983; Scriber, 1984). The tribe Troidini (in the subfamily Papilioninae) specializes on plants in the family Aristolochiaceae (Slansky, 1972; Scriber, 1984); Neotropical records from any other plant family in nature have not been confirmed, though may be possible since some Magnoliaceae are accepted by both *Battus* and *Parides* in the laboratory (Brown and Klitzke, unpublished). Aristolochiaceae species are also mostly tropical (Hoehne, 1942) and most contain aristolochic acids and benzylisoquinoline alkaloids, chemicals with noted pharmacological properties, including abortifascient and irritant of the gastro-intestinal tract of vertebrates (Hoehne, 1942; Von Euw et al., 1968; Chen & Zhu, 1987). Recently it has been shown that secondary compounds other than aristolochic acids and alkaloids are found in the roots, stems and leaves of south Brazilian *Aristolochia*

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species: lignans (Rücker et al., 1981), diterpenes (Habib & El-Sebakhy, 1981; Lopes et al., 1987; Lopes & Bolzani, 1988; Luiz et al., 1988), and essential oils (Leitão et al., 1988). Few studies have reported the effects of these plants or compounds on phytophagous insects (but see Miller & Feeny, 1983, 1989); very few herbivores other than Troidini are found feeding on *Aristolochia* (Rausher & Feeny, 1980; Rausher, 1981:6; Brown et al., 1981). Troidine larvae store toxic chemicals from their hostplants and pass them to the adults (Von Euw et al., 1968; Rothschild et al., 1970; Brown et al., 1981, 1991; Urzúa et al., 1983, 1987; Urzúa & Priestap, 1985), that are unpalatable to vertebrate predators (Brower & Brower, 1964; Brower et al., 1967; Rothschild, 1973; Brower, 1984; Chai, 1986, 1988). Both larvae and adults of troidines show aposematic coloration with Müllerian convergence, and serve as models for mimicry rings that include other Papilionidae and further Lepidoptera such as Pericopinae and Castniidae; some adults also resemble unpalatable ithomiine butterflies, and large *Pepsis* wasps (Brown, 1988; Aiello & Brown, 1988).

The natural history of American troidine communities has been studied in Brazil (Moss, 1919; D'Almeida, 1922, 1944, 1966; Brown et al., 1981; Otero & Brown, 1986) and western Mexico (Spade et al., 1988). Brown et al. (1981) discussed five sympatric species and their foodplants in the region of Campinas, interior of São Paulo state, and suggested the possible influence of host plant palatability and other factors in causing the different species proportions of troidines in different localities. The species showed varying acceptance for oviposition, and tolerance for larval feeding on the available *Aristolochia* hostplants in the field and laboratory (Brown et al., 1981; Otero & Brown, 1986). Other factors such as parasitism, predation, competition, phenology, adult resources, physical environment and evolutionary history were implicated in the variable composition of the guilds.

In this paper we seek to expand the data-base of Brown et al. (1981) by addressing the following questions raised there:

(1) Which environmental factors are important in determining the relative abundance of troidine species within the community? Is this abundance predictable? Is the hostplant involved?

(2) To what extent do different troidine species make use of different hostplants in different habitats? What are the causes and consequences of this?

In doing so, we hope to achieve a better understanding of the processes involved in community composition and dynamics at the Troidini/*Aristolochia* interface.

Materials and Methods

Studies were undertaken in a 3-ha well-watered forest garden (arboretum), "Monjolinho," and a larger (25-ha) tall *Eucalyptus* forest with a native middle- and understory, "Amarais," both in the Fazenda Santa Elisa of the Campinas Agronomical Institute, São Paulo (22°54' S., 47°05' W., about 650 m elevation), from 1980 to 1984. The two areas are separated by 1.0 km of cultivated fields

(Brown et al., 1981; Figure 1). Both contained many troidines during most of the year, in microhabitats resembling those occupied by the same species in fully natural systems (partly disturbed moist forests with abundant flowers).

The vegetation of Monjolinho (Figure 1), where juveniles were followed in 1981-1983, was mostly ornamental shrubs and trees, both native and introduced, with a dark and humid but well-developed understory in many parts of the woods, and an adjacent sunny garden with abundant flowers. The two major *Aristolochia* hostplants occurred in separated patches, consisting of 80 accessible *A. elegans* Masters and 42 *A. esperanzae* O. Kuntze, each population including individual plants ranging from small herbs to large climbers; five small plants of *A. arcuata* Masters were also present in Monjolinho. A single plot of 20 m² of *A. melastoma* Manso (about 40 rooted stolons) was experimentally introduced in 1981 from nearby Amarais, where *A. melastoma* and *A. arcuata* were abundant, and *A. elegans* and *A. esperanzae* absent. All these *Aristolochia* plants in Monjolinho were regularly examined for troidine juveniles, found on all of them at least once during this period (five high *A. elegans* vines remained inaccessible).

The troidine populations occurring in both study areas were *Battus polydamas* (L., 1758), *Parides proneus* (Hübner, 1825), *P. b. bunichus* (Hübner, 1822), *P. agavus* (Drury, 1782), *P. anchises nephalion* (Godart, 1819), and *P. neophilus eurybates* (Gray, 1852), as described in Brown et al. (1981). In both areas, adults were censused by weekly capture-mark-release-recapture periods, one hour in Monjolinho and two in Amarais (enough to visit at least twice all areas usually frequented by the butterflies), in the warmer part of the day, marking with indelible soft point pens of various colors (Sharpie, Sanford Corp.), with minimal handling to reduce trauma. Each individual was given a unique number, and note was taken of the species, sex, wing wear, location and time of day, and any unusual condition or behavior of the insect.

Two or three times a week, Troidini juveniles were sought in Monjolinho by thorough examination of leaves and stems of foodplants. Each egg or larva discovered was recorded and left on the original plant, to be observed on each subsequent visit until disappearance. The general yellow-orange color and similar size of the eggs of *P. bunichus*, *P. agavus* and *P. a. nephalion* precluded sure identification as to species until the end of the first instar, when the characteristic pattern of tubercles on the abdominal segments became conspicuous (Brown et al., 1981); the five larval instars were recognized by the width of their head capsules (Brown et al., 1981; Otero & Brown, 1986).

The minimum number of days that each larva stayed in each instar was determined as the period between the first and last observation in that instar. Means of these "minimums" were compared between species of Troidini and *Aristolochia*, using Student's *t*-test and one factor ANOVA. A chi-square test (or the Fisher exact probability when expected frequencies were five or fewer) was used to compare, on each species of hostplant, the numbers of larvae that survived to the third instar, in relation to those that "disappeared" before the end of the second instar (Sokal & Rohlf, 1981).

Results and Discussion

COMPARISONS OF THE SPECIES PROPORTIONS OF ADULT TROIDINES IN MONJOLINHO AND AMARAIS

Up through mid-1982, the species proportions of the troidine communities in Monjolinho and Amarais remained basically the same as those

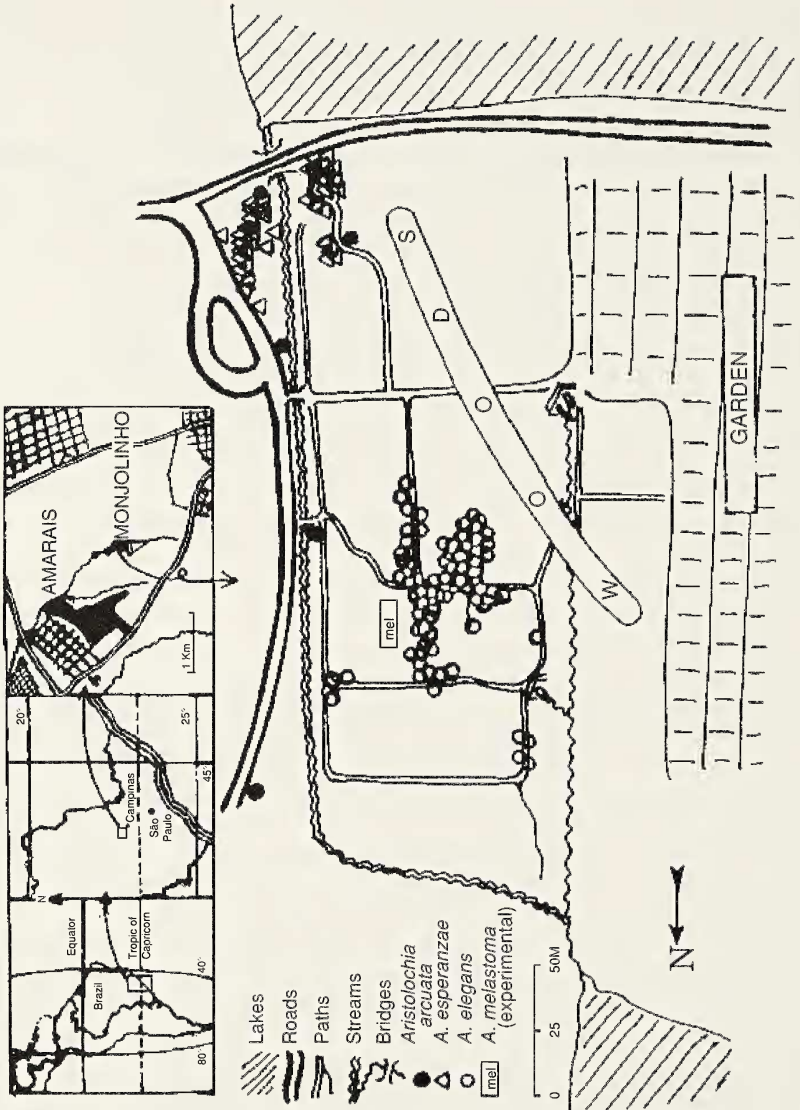


Figure 1. Map of Monjolinho, showing the location of individual *Aristolochia* plants followed in this study, and spatial relationship to Amaraís.

reported in Brown et al. (1981) (Table 1). Thus, while *P. proneus* represented over half the adults marked (1324 of 2420) in Amarais, and *P. agavus* represented only 3% (82) of that community, the abundance of the two was precisely reversed in nearby Monjolinho, where over half the adults marked (190 in 350) were *P. agavus*, and *P. proneus* represented but 3%. In Amarais, nine times as many *P. bunichus* and twice as many *B. polydamas* were marked as *P. a. nephalion*; in Monjolinho, the latter species was commoner than either of the former two. *P. neophilus* was only occasionally seen in both areas. By next-day recapture sessions, capture rates in Amarais were found to sample about 25-33% of the various *Parides* present and 10% of the *Battus* in two hours, while in Monjolinho, essentially all troidines present could be recorded in one hour (see Brown et al., 1981: 217). Exchanges of adults between the two sites occurred regularly (Table 1), indicating the possibility of choice of habitat and preferred resources in each.

In continued marking in the two localities from mid-1982 to mid-1984 (Table 1), these patterns remained relatively stable, though *P. proneus* doubled its abundance in Monjolinho, *P. a. nephalion* doubled its proportion in Amarais, *B. polydamas* became only half as common there and disappeared from Monjolinho, *P. bunichus* became rarer in Amarais, and the previously occasional visitor *P. neophilus* suddenly became a prominent resident (more than 20% of both communities), which it continues to be up until today (1991). All these changes were statistically significant (Table 1), with *P. agavus* remaining near its former proportions in both sites, and *P. proneus* stable in Amarais.

These alterations corresponded to a marked change in the rainfall patterns in 1982-1983, linked to a major El Niño-Southern Oscillation episode in the equatorial Pacific region (Rasmussen & Wallace, 1983; Barber & Chaves, 1983; Caviedes, 1984; Canby, 1984; Glynn, 1988). In south Atlantic manifestations of this climatic anomaly, over 2000 mm of rain fell in both years in Campinas, with very few dry months, representing an event never before recorded (only one other year since 1890 showed over 2000 mm—1970, with 2564—and it was flanked by two fairly dry years). Large areas of Amarais were flooded as a major new stream cut across the area, draining a nearby plateau. Elsewhere in Campinas, long-term flooding in the interior of old forests killed trees hundreds of years old, suggesting the rarity of such events. Such continuously rainy weather, promoting high humidity and extensive plant growth, could have reduced activity and population levels of *B. polydamas*, whose adults prefer dry, sunny habitats (Rausher, 1979; Brown et al., 1981), and whose gregarious larvae are especially prone to diseases which prosper under high humidity (Moss, 1919). These conditions are, however, typical of habitats preferred by *P. neophilus* in central Brazil and the Amazon Basin and Andean foothills. Such humidity may also have favored *P. a. nephalion* in Amarais, and been unfavorable to *P. bunichus*, a dry-area species (Brown et al., 1981; Otero & Brown, 1986).

Table 1. Adult individuals marked and recaptured in two adjacent Troidini communities during two periods, 1981-1984.

Species	Amarais (25 ha)					Monjolinho (3 ha)										
	Marks		Recaptures			Marks		Recaptures								
	(185 hr) end 1980- mid 1982	% (111 hr) of mid 1982- total mid 1984	% of 1982- total	Signifi- cance*	Total individu- als	(91 hr) 1981- mid 1982	% of total	% (55 hr) of mid 1982- end 1983	Signi- ficance*	Total individu- als	% of total	Transfers				
<i>Battus polydamas</i>	189	8	52	3	***	19	8	1	46	13	0	***	7	15	0	
<i>Parides proneus</i>	1324	55	925	52	-	504	22	1	10	3	19	*	7	24	3	
<i>Parides b. burnichus</i>	720	30	254	14	***	212	22	1	43	13	28	9	19	27	5	
<i>Parides agavus</i>	82	3	45	3	ns	31	24	2	190	54	155	48	-	130	38	4
<i>Parides anchises nephalion</i>	82	3	88	5	**	32	19	1	56	16	50	16	ns	33	31	1
<i>Parides neophilus eurybates</i>	23	1	401	23	***	109	26	3	5	1	68	21	***	32	44	0
Totals	2420	100	1765	100		907	(\bar{x} 22)	9	350	100	320	100		228	(\bar{x} 34)	13

* Difference in proportion of the local community between the two periods, significance tested by a 2 x 2 contingency table (chi-square, no correction) against the most abundant species in each community (*P. proneus* in Amarais, *P. agavus* in Monjolinho) using absolute numbers of marks. ns = not significant, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Thus, many of the small but significant changes in the community of adults during 1982-1984 could be tentatively correlated with a major macroclimatic change in that period. The contrasting abundances of *P. proneus* and *P. agavus* in the two sites remained evident, however, and reasons for this persistent difference in the two adjacent communities must be sought in other factors.

CHARACTERISTICS OF THE JUVENILE COMMUNITY IN MONJOLINHO

Between December 1981 and November 1983, 1802 troidine eggs and larvae were found and followed in Monjolinho (Table 2); 668 of these disappeared before the end of the first instar without being identified as to species. Only three pupae were encountered, in April 1982 and February-March 1983, all of *P. a. nephalion*, parasitized, and near the *A. elegans* on which they had been followed as larvae. While this could merely emphasize the usual dispersal of the larva far from the hostplant before pupation (thus escaping detection in the census periods), it also reflects the great mortality of juveniles in these species (Figure 2). Only 3% of all juveniles registered reached the final instar.

The numbers of juveniles found varied through the year, sometimes but not always showing peaks corresponding to, or a couple of months before the peaks in the adult population; both were markedly reduced in winter (June-August), when most of the population were in pupal diapause (D'Almeida, 1966; Brown et al., 1981). One fifth instar *P. a. nephalion* was followed in mid-winter, with little rainfall and temperatures between 5-25 °C, for eight weeks without showing notable growth, nor disappearing.

In 1981-1982 (Table 3), *Parides proneus* was the rarest of the juveniles, and *P. a. nephalion* was the commonest, with 50% more records than *P. agavus* (whose adults were four times as common as those of *nephalion*, Table 1) and three times as many as *P. bunichus* (equally common as adults). The period 1982-1983 was marked by large numbers of *P. neophilus* (Table 3), which led to an initial problem in separating its juveniles from those of *P. a. nephalion*, resolved only in mid-1983. Juveniles of *P. a. nephalion* and *P. neophilus* (probably about equal in number) both greatly outweighed those of *P. agavus*, while *P. proneus* juveniles increased significantly, presumably due to the introduction of their foodplant (*A. melastoma*), becoming just as frequent as those of *P. bunichus* and the diminished *B. polydamas*. These three were still less than half as common as *P. agavus*; unidentified eggs and first instar larvae increased from 24% to 38% of all juveniles. These juvenile proportions probably reflect both the abundance of adult females (Table 1) and of acceptable oviposition sites, as well as increased mortality of eggs and first instars due to heavy rain (Blau, 1980).

The relative deficiency of *P. agavus* juveniles in relation to the adult abundance (Table 3) could be due to their undetected presence on the

Table 2. Total eggs and larvae of Troidini encountered on *Aristolochia* species in Monjolinho, XII-1981 to XI-1983

HOSTPLANT: Stage of first encounter ^a	<i>Aristolochia elegans</i>					<i>Aristolochia esperanzae</i>					<i>Aristolochia melastoma</i>					<i>Aristolochia arcuata</i>																			
	0	1	2	3	4	5	sT	0	1	2	3	4	5	sT	0	1	2	3	4	5	sT	0	1	2	3	4	5	sT	0	1	2	3	4	5	
<i>Parides proneus</i>	29	14	2	1		46	3	1					4	11	10	2				1						24							0	74	
<i>Parides bunicichus</i>	16	27	9	8	2	2	64	14	6	1			21	1	3	1	3			8	1					8							1	94	
<i>Parides agavus</i>	89	55	14	7	4	169	32	17	5	5	1	1	61			2			2	2	1	2			2							3	235		
<i>Parides anchises</i>	3	17	10	3	3	1	37	34	20	13	6	7	80	1	2	1			4														0	121	
<i>nephalion</i>																																			
<i>Parides neophilus</i>	61	37	2			100	10	8					18	1					1							1							4	123	
<i>eurybates</i>																																			
<i>Parides anchises</i>	24	145	14	7	2	2	194	41	49	5	4	1	1	101	22	2	2		26	1	13					26	1	13				1	15	336	
+ <i>neophilus</i>																																			
<i>Battus polydamas</i>	61	18	6	6	1	92	39	10					49	10					10														0	151	
TOTAL (identified)						702							334						75														23	1134	
Unknown <i>Parides</i>	290	119				409	183	35				218	13	3				16															25	668	
(eggs + first)																																			
TOTAL (all juveniles on each plant)						1111						552						91																48	1802

^a 0 = eggs, 1 to 5 = first to fifth instar larvae; sT = subtotal for each species on each hostplant.

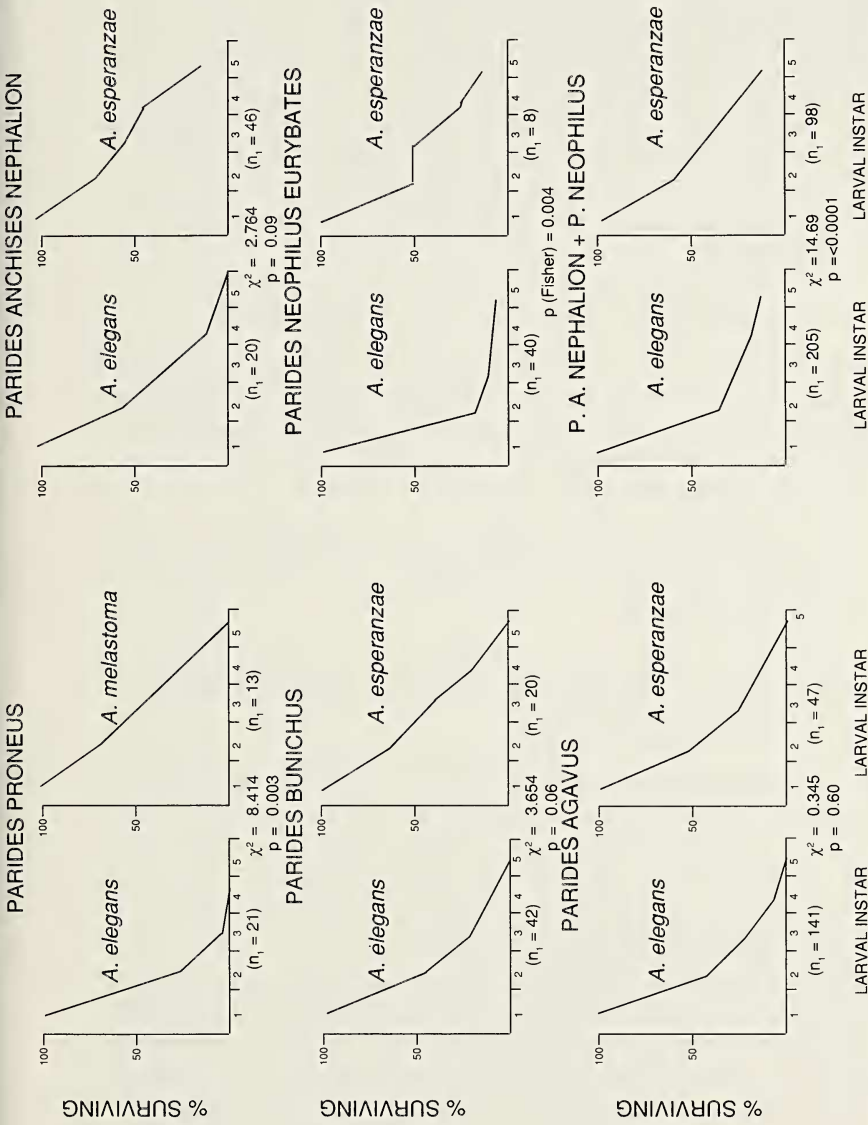


Figure 2. "Survival" of larvae (first to fifth instars) of various *Parides* species (and of indistinguishable *P. a. nephalion* and *P. neophilus*) on different *Aristolochia* species in Monjolinho. The probabilities represent survival to the molt to the third instar (see text), which is always higher in the right-hand graph of the pair; note that more eggs are always placed on *A. elegans*, the species with the greatest biomass (left-hand graphs), except for *P. a. nephalion* (upper right pair), but this plant always gave lower survivorship than the alternative hostplant, for all species of troidines.

Table 3. Juveniles of Troidini discovered in Monjolinho, 1981-1983.

Species	1981-mid 1982			% all juv.	mid 1982-end 1983			% all juv.	Signifi- cance*
	Eggs	Larvae	Total		Eggs	Larvae	Total		
<i>Battus polydamus</i>	79	42	121	23	66	12	78	6	***
<i>Parides proneus</i>	0	6	6	1	43	28	71	5	***
<i>Parides b. bunichus</i>	4	40	44	8	29	41	70	5	ns
<i>Pariedes agavus</i>	31	66	97	18	98	70	168	12	-
<i>P. anchises nephalion</i>	43	99	142	26	6	7	13	1	} ns
<i>P. neophilus eurybates</i>	0	0	0	0	76	47	123	9	
<i>P. (anchises nephalion</i> <i>+ neophilus eurybates)</i>	0	0	0	0	88	248	336	24	***
Unidentified <i>Parides</i> species (less <i>proneus</i>)	101	28	129	24	408	131	539	38	***
Totals	258	281	539	100	814	584	1398	100	

* Difference between census periods, compared against *P. agavus* (most abundant species as adults). The clustered eggs of *polydamus* reduce the validity of the statistical test, which nevertheless would not lose significance. Non-significance for *P. a. nephalion* occurs for all proportions between 0.49 and 0.97 in the mixed batch (336 juveniles) with *P. neophilus*. ns = not significant, *** = $P < 0.001$.

highest *A. elegans* vines; *P. a. nephalion* preferred the small, easily inspected plants of *A. esperanzae* for oviposition, where the larvae were easily discovered and followed.

DIFFERENTIAL SURVIVORSHIP OF TROIDINE JUVENILES ON THE VARIOUS FOODPLANTS

Troidine larvae usually stay on the hostplant nearest to where they hatch from the egg as long as suitable leaves are available, only leaving it to seek other foodplants in later instars if necessary (Rausher, 1981; Brown et al., 1981). Even so, 97% of all juveniles observed in 1981-1983 (1748 of the 1802) disappeared before attaining the fifth instar; larger larvae were sometimes found on neighboring plants (*Aristolochia* and others), but in general "disappearance" meant death.

Arthropods (ants and small spiders) were the principal larval predators in Monjolinho, also observed in the laboratory by Brown et al. (1981) (see also Watanabe, 1976, 1981; Hirose et al., 1980; Rausher, 1981; and Feeny et al., 1985). Attack on later instars by vertebrates, observed by all these authors, was not recorded in Monjolinho; fifth instar mortality in *P. anchises nephalion* and *P. neophilus* occurred through parasitoids, also recorded for eggs, larvae and pupae by Moss (1919) and the above authors. Parasitism and cannibalism by congeners, indicated by most of these studies, were not quantified in Monjolinho.

The "quality" of the hostplant can make important contributions to juvenile survivorship and mortality (Scriber & Feeny, 1979; Price et al.,

1980; Scriber & Slansky, 1981; Courtney, 1981; Williams et al., 1983; Rhoades, 1985). Troidine juveniles were encountered in different numbers and proportions on their four available foodplants (Table 2). *Parides agavus* predominated on *A. elegans*, on which *P. neophilus* was more common than *P. a. nephalion*, but the last species was dominant on *A. esperanzae*. *P. proneus* predominated on *A. melastoma* but was absent from *A. arcuata*, on which *B. polydamas* was also absent, possibly due to its very small biomass in Monjolinho (five small, scattered plants).

Table 4 shows the mean minimum duration (in days) for each instar of *Parides* on each *Aristolochia* species in Monjolinho. The apparent general tendency for more rapid development on *A. esperanzae* in relation to *A. elegans* was significant only for the first larval instar of *P. agavus*, and in any case may have been due to the softer, perhaps more nutritious leaves on the generally younger plants of *A. esperanzae*. The lower means of *P. proneus* on *A. melastoma* did not reach significance. Not enough larvae were marked and followed continuously to permit simultaneous comparisons of larval survivorship on the four species of hostplants.

Figure 2 shows the percentage of larvae of each *Parides* species surviving on each hostplant (in pairs), from first to fifth instars (fourth in *P. proneus*). While *P. agavus* did equally well on both *A. elegans* and *A. esperanzae*, larvae of *P. bunichus* and *P. a. nephalion* survived better to the third instar on *A. esperanzae* (with marginal significance, $P=0.06$ and 0.09), and *P. neophilus* and the mixed ($\approx 1:1$) lot of *P. a. nephalion* and *P. neophilus* had significantly higher survivorship on *A. esperanzae* than on *A. elegans*. This might indicate a better "quality" for the former plant, at least in Monjolinho where it is represented mostly by young, soft plants. *P. proneus* did much better ($P=0.003$) on its natural foodplant *A. melastoma* than on the far more abundant *A. elegans*, where females deposited the majority of their eggs.

These different reactions of larvae of each species to the various foodplants chosen by their mothers are better seen in Figure 3, in which the ability to survive is emphasized as percent of total larvae remaining on each plant species as the larvae grow through each instar. The figure reveals the superior relative survival of *P. proneus* on *A. melastoma* over other hosts, of *P. agavus* and younger *P. neophilus* on *A. esperanzae* (though the more abundant *A. elegans* was preferred for oviposition, see Table 2 and Figure 2), and of *B. polydamas* and *P. bunichus* on *A. elegans*. Some patterns are easier to discern in Figure 3 than in Figure 2; note especially, in the later instars of *P. bunichus*, *P. a. nephalion* and *P. neophilus*, the reversion of the lower survival patterns on *A. elegans* in the early instars.

A preliminary investigation of hostplant chemistry (Morais, 1986) showed a general absence of aristolochic acids in the leaves of *A. elegans* and *A. esperanzae*, confirming results of Hussein & El-Sebakhy (1974) and Urzúa & Priestap (1985) (these substances are common in the roots of these same plants—see Priestap et al., 1971—and are known to have

Table 4. Mean number of days for each larval instar of *Parides* species on different *Aristolochia* species in the field (Monjolinho).

Species and Instar	<i>A. elegans</i> $\bar{x} \pm s$	(n)	<i>A. esperanzae</i> $\bar{x} \pm s$	(n)	<i>A. melastoma</i> $\bar{x} \pm s$	(n)	"t" or ANOVA ^a
<i>P. proneus</i> egg	6.60 ± 2.93	(19)	5.67 ± 1.15	(3)	3.67 ± 1.51	(6)	(all 3) NS (el × mel)**
first larval	7.37 ± 6.67	(8)			6.67 ± 2.34	(6)	NS
second larval	5.83 ± 4.07	(6)			3.50 ± 2.14	(8)	NS
<i>P. bunichus</i> egg	6.71 ± 2.63	(7)	6.0 ± 2.51	(8)			NS
first larval	7.97 ± 4.98	(31)	6.29 ± 1.72	(17)	6.50 ± 3.54	(2)	NS
second larval	5.50 ± 3.25	(8)	5.50 ± 2.17	(10)			NS
third larval	3.60 ± 2.61	(5)	3.60 ± 2.07	(5)			NS
fourth larval	4.0 ± 2.64	(3)	3.50 ± 2.12	(2)	5.33 ± 1.53	(3)	NS
fifth larval	8.0 ± 5.57	(3)					-
<i>P. agavus</i> egg	7.08 ± 3.30	(73)	5.91 ± 1.90	(22)			*
first larval	8.46 ± 4.68	(116)	5.91 ± 3.14	(32)			**
second larval	5.60 ± 2.72	(42)	5.18 ± 3.52	(11)			NS
third larval	4.95 ± 2.76	(19)	5.17 ± 3.19	(6)			NS
fourth larval	4.73 ± 2.53	(11)	3.0 ± 0.0	(2)			-
<i>P. anchises</i> egg			6.40 ± 2.51	(5)			
first larval	6.75 ± 5.68	(4)	6.0 ± 3.54	(8)			NS
second larval	6.20 ± 3.77	(5)	5.70 ± 3.33	(10)			NS
third larval	5.0 ± 2.83	(2)	3.0 ± 0.0	(3)			-
fourth larval	6.40 ± 1.95	(5)	5.0 ± 2.52	(7)			NS
fifth larval	10.83 ± 5.12	(6)	4.75 ± 1.98	(8)			*
					<i>A. arcuata</i>		
<i>P. neophilus</i> egg	5.63 ± 3.48	(38)	4.44 ± 1.81	(9)	5.67 ± 2.31	(3)	NS
first larval	6.29 ± 4.28	(55)	5.62 ± 2.20	(8)	4.67 ± 2.08	(3)	NS
second larval	5.50 ± 3.39	(14)	4.0 ± 0.0	(2)			-
third larval	10.0 ± 4.32	(4)					-
fourth larval	4.25 ± 3.30	(4)	2.0 ± 0.0	(2)			-

^a NS = Not significant, * = $p < 0.05$, ** = $p < 0.01$.

effects on troidine larval performance—Miller & Feeny, 1989). Benzylisoquinoline alkaloids (El-Sebakhy & Waterman, 1984), also important in larval feeding (Miller & Feeny, 1983, 1989) were variable, but most abundant in *A. elegans*. Several other secondary chemicals could be detected in the leaf fractions, different in each species. Extracts of *Aristolochia* leaves were seen to turn very dark with great rapidity in the presence of air, indicating phenolic polymerization; the compounds responsible for this were not isolated.

It is clear that evaluation of the possible influences of leaf secondary chemistry on the variation in larval performance (Figures 2-3) and preference for different species must await more detailed investigations and bioassays (these authors, P. E. R. dos Santos & C. Klitzke, in progress).

Since the larvae were not all observed simultaneously in the field, it is not possible to extrapolate the relative global performance of the species

over two years on each plant to draw any conclusions about competitive ability. Maps of the use of individual *A. elegans* and *A. esperanzae* (based on Figure 1) by each troidine species showed appreciable concentration and overlap of species on certain plants over the period. These were often individuals of greater biomass or permanence in the system. Globally, *A. esperanzae* was occupied predominantly by final instar larvae of *P. a. nephalion*, and *A. elegans* by fifth instar *Battus polydamas* (Figure 3). Although these data might indicate a reasonable potential for competitive interaction among the species on both plant populations in Monjolinho, the results did not permit rejection nor sustaining of the hypothesis of resource partitioning due to competitive interaction, sufficient to affect species proportions in the community, distinguishable from the effects of tolerance, oviposition preference, growth rates and other factors mentioned.

Finally, a density-independent factor causing juvenile death, especially on young *A. esperanzae* plants near the entrance to Monjolinho (Figure 1), was human interference during the observations and in periodical cutting of these "weedy" plants by the caretakers. These plants were always greatly preferred by *P. a. nephalion* juveniles, that could have suffered excessive reductions in the larval stage due to this factor, leading to lower adult abundance (Table 1).

INFLUENCE OF THE PHYSICAL ENVIRONMENT ON *P. AGAVUS*

While variations in species proportions of five of the six troidines in Campinas have been tentatively correlated with macroclimate and larval foodplants, no factor yet discussed was adequate to explain the consistent great difference in abundance of *P. agavus* between Monjolinho and Amarais (Table 1).

Microclimate is also important to troidines, including in the laboratory where it can determine adult activity, larval survivorship and pupal diapause (Brown et al., 1981). Because *P. agavus* is more restricted to the dense humid Atlantic forests than the other members of the community in Campinas, it could be more sensitive than these to light structure and humidity. Microclimatic measurements in the understories of Monjolinho and Amarais showed no significant difference in humidity, but appreciably more illumination in the latter site, especially in the midday hours (Morais, 1986). Thus, the different vegetation structures in the two areas affect the quality and quantity of light in the understory, recognized as an important physical factor for insect species (Warren, 1985), including troidines (Moss, 1919; Rausher, 1981; Brown et al., 1981).

The influence of vegetation/light structure *versus* larval foodplant on the proportion of *P. agavus* in the community might be tested in additional sites, such as ones with the foodplants of Amarais and the dark understory of Monjolinho, or with a brightly lit understory and the plants of Monjolinho. The latter habitat, often with abundant *A. elegans* and/or *A. esperanzae*, is very frequent in the disturbed interior region of São Paulo; *P. bunichus* and *B. polydamas* are predominant in these sites,

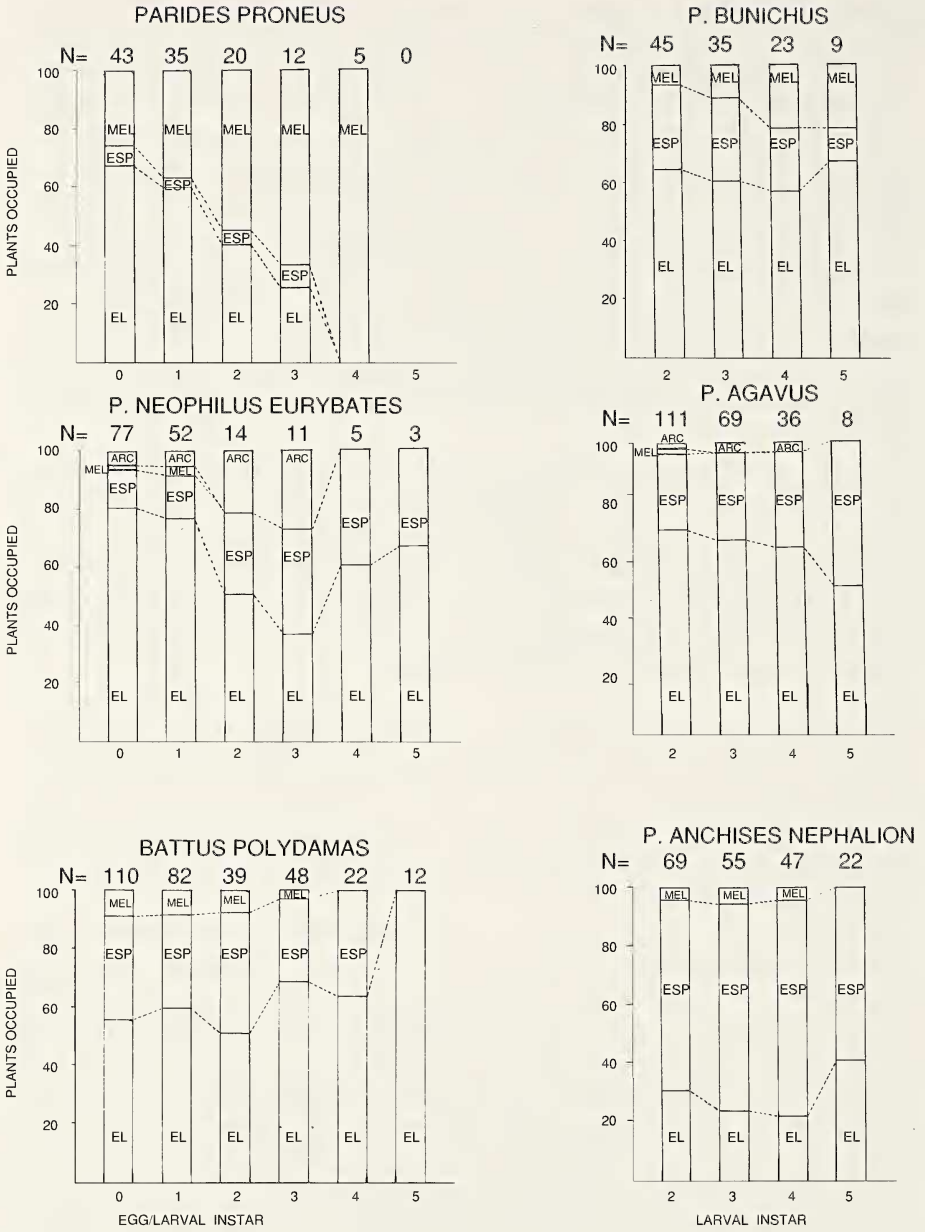


Figure 3. Percentage of eggs and larvae (by instar) of each troidine species found on each different *Aristolochia* hostplant. Eggs and first-instar larvae of *P. bunichus*, *P. agavus* and *P. a. nephalion* could not always be surely separated from each other, and therefore are omitted.

with *P. a. nephalion* and *P. neophilus* variably present in more humid riverine areas, and *P. agavus* at best very occasional. In contrast, six well-studied sites in the interior of São Paulo with reduced understory illumination, from 400 to 1300 m elevation and with a wide variety of *Aristolochia* foodplants, all showed predominance of *P. agavus* in the troidine community. A notable example was the dense riverine tangle 800 m NNW of the main colonies of the Horto Florestal de Sumaré (Area "D" of Figure 1A in Brown et al., 1981: 201, 217), which contained principally *P. agavus*, mobile between this preferred area and the little-chosen, more open woods of the Horto, where it represented only 6% of the community—a situation almost parallel to that of Monjolinho and Amarais. While correlation does not mean causation, the circumstantial evidence suggests a strong influence of understory light structure and small effect of foodplant species on the abundance of *P. agavus* in the community.

CONCLUSIONS, SUMMARY AND PERSPECTIVES

In relation to the questions posed in the Introduction, this study showed that:

(1) Larval hostplant effect on the proportions of six species in the troidine guilds in southeastern Brazil was evident only in the case of *Parides proneus*, whose abundance corresponded to that of its principal hostplant, *Aristolochia melastoma*.

(2) An unusual period of increased and continuous rainfall, associated with a very strong El Niño episode in 1982-1983, was accompanied by significant reduction in abundance of *Battus polydamas* in two communities, and a decrease of *Parides bunichus* and increase of *P. anchises nephalion* in one of them. The same factor may have encouraged a range expansion of *P. neophilus*, to become the second most common species in both communities, in which it was previously only an occasional visitor.

(3) A denser structure of the vegetation, with corresponding reduction of light in the understory, correlated with the abundance of *P. agavus* in diverse habitats with a variety of potential hostplants available.

(4) All of the species except *P. proneus* could feed and grow on all four common *Aristolochia* hostplants present in the two habitats studied; some differences in larval performance detected may be due more to chance or the age and size of the foodplants used, rather than to plant chemistry or general "quality."

(5) No evidence was found for partitioning of hostplants or their parts between the species (except for *P. proneus*), even though this phenomenon may exist in natural systems where *Aristolochia* is rarer (Moss, 1919). This suggests that Troidini are usually quite opportunistic in foodplant usage within the *Aristolochia* available, as found by Spade et al. (1988) in western Mexico.

Present work is directed towards details of foodplant chemistry, including controlled feeding experiments with fractions and isolated com-

pounds, especially from the least acceptable *A. galeata* (= *brasiliensis*) and *A. gigantea* (Brown et al., 1981), not present in Monjolinho or Amarais. The importance of parasitism and predation will also be evaluated experimentally with split cohorts of juveniles on various foodplants in different habitats. Further data may come from experiments and observations over long periods in natural habitats where the Troidini and their foodplants are rarer, and perhaps thereby subjected to large effects from small variations in various environmental factors.

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